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ANTILLEAN SHORT-EARED OWLS INVADE SOUTHERN FLORIDA

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ABSTRACT.—Recently, Short-eared Owls (*Asio flammeus*) have invaded extreme southern Florida during spring and summer, most appear to be post-fledging dispersers. Morphological and plumage characteristics identify the specimens as coming from the Antilles, most likely from Cuba, where numbers and range have expanded greatly in recent years. This dispersal continues a trend that began in other bird species more than half a century ago. Since 1932 about one landbird species per decade has colonized southern Florida from the Antilles. *Received 27 May 1998, accepted 30 Nov. 1998.*

During the last two decades, Short-eared Owls (*Asio flammeus*) have occurred with increasing frequency in extreme southern Florida, especially from March through September. In the absence of specimens, these reports were assumed to represent individuals of the nominate race *A. flammeus flammeus,* which was the only form of this polytypic species known from the North American continent. *Asio f. flammeus* is Holarctic; in the western hemisphere it breeds in northern North America and migrates south as far as southern United States, Mexico, and rarely the West Indies (American Ornithologists' Union 1957, 1998). During the 1990s we obtained several specimens of Short-eared Owls from extreme southern Florida. Here we summarize all recent records and reports of Short-eared Owls from southern Florida, describe the characteristics of Holarctic and Antillean Short-eared Owls and conclude that most of the recent spring–summer records are from an Antillean population, and briefly review their nomenclature. Finally, we discuss possible causes for the dispersal of these owls into Florida and their potential for colonizing the North American continent.

SPECIMENS, PHOTOGRAPHS AND REPORTS

Specimens.—Between July 1990 and March 1998, we obtained eight dead Short-eared Owls from the Florida Keys, Monroe County, Florida. Three of the six males showed no molt, while three showed light, scattered body molt. All six males had small testes and all had extensive black feathering around the eyes, which in the nominate race typifies juvenal plumage (Holt and Leisure 1993). One female (GEW 5902, 25 May 1996, ovary 15 × 4 mm, largest ovum 1 mm, substantial body molt) also appeared to be juvenile, but the other (GEW 5889, late April 1994, ovary 17 ×

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FRONTISPIECE. Antillean Short-eared Owl photographed in Ft. Zachary Taylor State Park, Key West, Monroe County, Florida on 4 April 1994 by Wayne Hoffman.

4, largest ovum 2 mm) had worn plumage and possibly a regressing brood patch, and might have been an adult.

Comparative material included five Short-eared Owl specimens from the Antilles, four from the southern Florida mainland, and 46 from elsewhere in North America. In June 1995 Orlando Garrido kindly loaned us an unsexed adult specimen (MNHN-1595) collected in Sancti Spiritus Province, Cuba. In 1996 Garrido donated to the Archbold Biological Station collections a male specimen collected near Havana (GEW 5925). We also examined two nestlings collected in the Dominican Republic in November 1963 (LSUMZ 142354 and 142355; Schwartz and Klinikowski 1965). The four mainland specimens, all from Dade County, were two from Everglades National Park (EVER 5035, collected 5 January 1971; GEW 5890, collected 9 December 1990) and two in the University of Miami Research Collections (UMRC 948, collected 7 February 1956; UMRC 5387, collected 8 November 1966), which now are in the collections at Archbold Biological Station.

In April 1997, Hoffman measured six specimens of the Holarctic *Asio flammeus flammeus* in the Pennsylvania State University collections and 40 specimens in the Carnegie Museum collections. All were taken in North America throughout the year. The few specimens with missing or incompletely grown primaries or central rectrices were excluded from analysis. Hoffman also examined and measured the single Puerto Rican specimen in the Carnegie Museum.

Measurements taken include lengths of wing (flattened), tail, tarsus, and culmen from the cere. Measurements were taken as described by Palmer (1962) and Cramp and coworkers (1977). Tarsi are difficult to measure on the feathered feet of owls, so a dissecting probe was used to assist in locating the measuring points on the posterior of the intertarsal joint and the anterior of the middle toe articulation with the tarsometatarsus.

Photographs and reports.—We examined photographs of six individuals that did not become specimens: three from the Dry Tortugas, two from other of the Florida Keys, and one from the Gulf of Mexico off Hernando County. We reviewed reports of Short-eared Owls from Florida published in *Audubon Field Notes* and *American Birds* (Loftin et al. 1991) and evaluated other written and verbal reports of these owls in southern Florida since 1978.

RESULTS

Current status of Short-eared Owls in southern Florida.—Our review of citations in *Audubon Field Notes* and *American Birds* yielded about 68 reports of Short-eared Owls in Florida before 1978. With one exception, a bird seen 14 June 1963 at Lakeport, Glades County, all pre-1978 reports were of occurrences between early October and late March. We obtained information on 30 occurrences of 33–37 Short-eared Owls in Florida since 1978, including 16 records (specimens and photographs) and 14 reports (no tangible evidence). Twenty-three of the 30 appeared in spring and summer, outside the early October–late March dates dominating the earlier period. During spring–summer 1994 the influx seemed particularly heavy. The first bird was located at Ft. Taylor State Recreation Area in Key West, 25 March (photographed on 4 April). It was joined by a second bird in mid-April; both disappeared by mid-May. Meanwhile a birding tour located three birds at the Dry Tortugas on 8 April (Woolfenden, pers. obs.). One was picked up there in weakened condition on 18 April and died while in transit to Key West for treatment (GEW 5889). On 8 June, W. B. Robertson, Jr. flushed a group of four owls on Long Key, Dry Tortugas. Thus, a minimum of five, possibly as many as nine, owls were found in southern Florida in spring 1994. Another record that summer was of an individual plucked from the water offshore of Hernando Co., in June (Table 1). The dates of occurrence of these records and reports suggest a source other than the Holarctic. The specimens we have obtained allowed us to test this hypothesis using geographic variation described for Short-eared Owls.

Structural and plumage differences between the Antillean and Holarctic Short-eared Owls.—Based on Ridgway (1914) and Wetmore (1928), and the specimens we examined, Antillean Short-eared Owls differ from Holarctic Short-eared Owls in size, proportions, and plumage. These differences appear adequate to distinguish all specimens in the hand, and to allow identification of birds observed closely in the field. They also appear sufficient

TABLE 1. Short-eared Owl records and reports from southern Florida since 1978.

Year	Dates	Location	Source	Documentation	Origin
1978	21–22 Jun.	Dry Tortugas	Hoffman et al. 1979	Photographs	Antilles
1979	24 Nov.	Virginia Key	Am. Birds 34:154	—	—
1984	Winter 1983–84	Flamingo	P. and M. Brown, pers. comm.	—	—
1984	11–12 Apr.	Dry Tortugas	Am. Birds 38:901	—	—
1984	30 Dec.	ENP main road	Am. Birds 39:160	—	—
1985	27–29 Apr.	Dry Tortugas	Am. Birds 39:290	Published photograph	Antilles
1986	19–21 Apr.	Dry Tortugas (2 birds)	Am. Birds 40:461	—	—
1987	late Mar.–25 May	Dry Tortugas	Am. Birds 41:421	—	—
1987	24 Aug.	Bottle Key, Florida Bay	R. Bowman, P. Cavanagh, pers. comm.	Photographs	Antilles
1988	Aug.	Big Pine Key		Specimen, lost	Antilles?
1989	26 Apr.	Big Pine Key	W. B. Robertson, Jr., pers. comm.	Wing & leg saved, ENP	Antilles
1989	5 May	Dry Tortugas	Am. Birds 43:469	—	—
1990	28 Jul.	Dry Tortugas	M. Eng, pers. comm.	Specimen, ABS, GEW 5861	Antilles
1990	10 Dec.	ENP main road		Specimen, ABS, GEW 5890	Holarctic
1992	10 Apr.	Key West		Specimen, ABS, GEW 5862	Antilles
1993	18 Apr.	Marathon		Specimen, ABS, GEW 5886	Antilles
1993	10 Jun.	Dry Tortugas (2 birds)	W. B. Robertson, Jr., pers. comm.	—	—
1994	25 Mar.–early May	Key West (2 birds)	F. & J. Cheeseman, pers. comm.	Photographs	Antilles
1994	8 Apr.	Dry Tortugas (3 birds)	G. E. Woolfenden	Specimen, ABS, GEW 5889	Antilles
1994	8 Jun.	Dry Tortugas (4 birds)	W. B. Robertson, Jr., pers. comm.	—	—
1994	early Jun.	off Hernando Co.	R. Collins, pers. comm.	Photographs	Antilles
1994	3 Sept.	Sugarloaf Creek	W. Hoffman	—	—
1994	1 Nov.	Dry Tortugas	W. B. Robertson, Jr., pers. comm.	—	—
1995	11 Mar.	Key West		Specimen, ABS, GEW 5892	Antilles
1995	26 Jul.	Grassy Key		Specimen, ABS, GEW 5900	Antilles
1996	25 May	Marathon		Specimen, ABS, GEW 5902	Antilles
1996	17 Jul.	Marathon	S. Culley, pers. comm.	—	Antilles
1997	28 April	Dry Tortugas	D. Friedman, pers. comm.	Photographs, D. Friedman	Antilles
1998	12 March	Key Largo		Specimen, ABS, GEW 5930	Antilles
1998	17 April	Dry Tortugas	W. Hoffman	—	Antilles
	Totals	32–37 birds	—	8 specimens	Antilles
				6 photographic	Antilles
				1 specimen	Holarctic

TABLE 2. Measurements of Short-eared Owl specimens. All measurements (in mm) taken by Hoffman. Statistical comparisons of means are by Student's *t*-test (*t*), unpaired. Probability (*P*) of equal means is two-tailed.

		A. f. flammeus			West Indian				
Measurement	Sex	*n*	Mean	(Range)	*n*	Mean	(Range)	*t*	*P*
Wing	M	25	313.8	(306–323)	8	289.8	(286–291)	13.77	<0.001
Wing	F	24	316.3	(308–325)	3	294.7	(292–299)	8.30	<0.001
Wing	both	49	315.0	(306–325)	11	291.0	(286–299)	16.05	<0.001
Tail	M	25	142.0	(133–148)	8	132.8	(127–141)	5.51	<0.001
Tail	F	24	146.1	(134–153)	3	140.7	(136–146)	1.68	>0.05
Tail	both	49	144.0	(133–153)	11	134.9	(127–146)	5.25	<0.001
Tarsus	M	25	42.7	(38–46)	8	52.2	(50–53.5)	10.28	<0.001
Tarsus	F	24	43.7	(39–46)	3	50.7	(50–54)	5.55	<0.001
Tarsus	both	49	43.2	(38–46)	11	51.8	(50–54)	11.67	<0.000
Culmen	M	24	26.3	(24.0–28.0)	8	28.9	(27.8–29.6)	5.21	<0.001
Culmen	F	24	26.2	(24.0–28.3)	3	29.8	(29.5–30.1)	4.51	<0.013
Culmen	both	48	26.3	(24.0–28.3)	11	29.1	(27.8–30.1)	6.94	<0.001

to distinguish Antillean specimens from all other members of *Asio flammeus*.

Compared to Holarctic *Asio f. flammeus*, Antillean Short-eared Owls have shorter wings and tails, longer tarsi, and slightly larger bills (Table 2). Male and female *A. f. flammeus* overlapped broadly for all measurements, and the Antillean male and female specimens overlapped broadly in tail and tarsus measurements. No overlap existed between *A. f. flammeus* and the Antillean specimens in length of the wing, tarsus, and culmen. The two populations overlapped substantially only in tail length. Because of the broad overlap between the sexes for most measurements, tests of significant mensural differences between the groups were run for both sexes combined as well as for males and females separately. Differences between the groups were highly significant for all comparisons except tail length among females (Table 2). Hoffman's measurements of *A. f. flammeus* specimens are similar to those published in Cramp and coworkers (1985), except that the culmen measurements averaged 3 mm shorter, suggesting a methodological difference. Ridgway (1914), Wetmore (1928), and Garrido (1984) have published wing measurements for Antillean owls, and Marshall (pers. comm.) provided measurements on six specimens at the US National Museum (Table 3). Together, these sources provided measurements of 15 specimens (five males, three females, seven unsexed); wing lengths ranged from 274 to 300 mm, which are similar to ours (286–299 mm).

The most notable plumage differences involve coloration of the upper back and the underparts (Fig. 1). On Holarctic birds the contour feathers of the upper back, between and anterior to the scapulars, are mostly tawny with a dark brown central stripe. On Antillean birds these back feathers are mostly dark brown with tawny edgings. As a result the upper back of Holarctic birds appears distinctly striped, whereas the backs of Antillean birds appear overall dark brown, or dark brown with obscure tawny mottling. The underparts of *A. f. flammeus* are heavily streaked with dark brown on a pale tawny to whitish background (Fig. 1). Streaks are broadest and most dense on the upper breast, and gradually become narrower and more sparse posteriorly. The streaked feathers most posterior are located on or near the knee joints. The underparts of the Antillean owls are much more buffy overall. The streaking is similar on the upper breast, but abruptly becomes much narrower and more sparse at mid-breast. The lower breast and belly are mostly unstreaked with a few narrow streaks (less than 2 mm wide) on the flanks. The feathering on and around the knee joints is unstreaked. The difference in pattern and coloration of the underparts was noted as early as 1770 (Buffon *in* Wetmore and Swales 1931). Other plumage differences include the color of the upper tail coverts (fairly dark brown in Antillean birds versus

TABLE 3. Measurements (in mm) of Short-eared Owls, from the literature.

Sex	Taxon	*n*	Wing[a]	Tail[a]	Tarsus[a]	Culmen[a]	Source
Male	*flammeus*	varies[b]	315 (304–326)	142 (134–152)	44.5 (42.8–46.0)	28.5 (27.5–29.4)	Cramp and coworkers 1985
	domingensis	1	294				Wetmore 1928
	portoricencis	2	283 (280–285)				NMNH 573526, 354499
	Cuban	2	280, 285				NHMH (on loan)
Female	*flammeus*	varies[c]	319 (309–331)	144 (137–154)	46.2 (44.5–48.1)	29.0 (27.7–29.8)	Cramp and coworkers 1985
	domingensis	1	298				Wetmore 1928
	portoricensis	2	285				NMNH 358579, 307978
Unsexed	Cuban	varies[d]	292 (285–300)	140		?[e]	Garrido 1984
	portoricensis	4	277 (274–281)				Wetmore 1928
	portoricensis	varies[f]	278 (274–286)	131 (126–136)		?[e]	Ridgway 1914

[a] Mean (range).
[b] $n = 39$ for wing and tail; $n = 16$ for tarsus and culmen.
[c] $n = 28$ for wing; $n = 32$ for tail; $n = 14$ for tarsus; $n = 12$ for culmen.
[d] $n = 3$ for wing; $n = 1$ for tail.
[e] Ridgway (1914) and Garrido (1984) measured culmen only to the cere. Ridgway reported mean = 17.3 mm ($n = 3$) and Garrido 17.3 mm ($n = 1$). In comparison, Cramp and coworkers (1985) reported means to cere of 16.7 mm (16 males) and 16.9 mm (12 females) for *A. f. flammeus*.
[f] $n = 3$ for wing; $n = 4$ for tail.

tawny yellow in *A. f. flammeus*). The sides of the head just behind the lateral edges of the facial disk have an unmarked brown patch not found in *A. f. flammeus*. The dark bars on the rectrices also tend to be more complete and have straighter margins in the Antillean birds.

The feathering of the feet also differs between Holarctic and Antillean birds. In *Asio f. flammeus* the tarsi and the upper surfaces and sides of the toes are densely covered by fine tawny feathers. On Antillean birds, the feathering of the toes is restricted to the dorsal surfaces and terminates 3–6 mm from the talons. The featherless skin of the under surfaces extends up the sides of the toes to near their tops. Feathering on the toes is also more sparse, with exposed skin showing between individual feathers on museum specimens. The feathers on the tarsi and toes are shorter in the Antillean birds (ca 6 mm versus 16 mm on the posterior surface midway along the tarsus and ca 3 mm versus 6 mm long on the proximal phalanx of the middle toe).

Photographs of the Antillean owls appear to show more prominent "ear" tufts than do *A. f. flammeus,* but an attempt to measure the tufts on the specimens at ABS failed to show differences (tuft length 19–29 mm for 10 Antillean owls; 20–27 mm for 3 *flammeus*). The surrounding head feathers appeared shorter on the Antillean birds so the tufts may in fact protrude farther, and possibly the Antillean owls are more likely to erect the tufts when confronted by photographers.

The Antillean birds appear to weigh substantially less than northern birds. Three seemingly non-emaciated males of our Florida specimens weighed 260 g, 280 g, and 299 g, and the two non-emaciated females 274 g and 288 g. In comparison, mean weights of *A. f. flammeus* are 315 g for males, and 378 g and 411 g for two samples of females (Holt and Leasure 1993).

Comparison of southern Florida specimens with a series from the Greater Antilles.—We sent the first two specimens we obtained (GEW 5861 and GEW 5862) to Joe T. Marshall at the National Museum of Natural History (NMNH) who compared them with a series of eight specimens from the Greater Antilles (six from Puerto Rico and two from Cuba). He informed us (pers. comm.) that the Florida specimens were similar to these An-

FIG. 1. Specimens of *Asio f. domingensis* and *Asio f. flammeus*. A. Dorsal view. Left row from top: *Asio. f. domingensis*; 1 unsexed adult from Cuba, 1 female from Florida, and 4 males from Florida. Right row from top: *Asio. f. flammeus*; 3 females from mainland southern Florida, 1 female from Grand Turk. B. Ventral view. Left row from top: *Asio. f. domingensis*; 1 unsexed adult from Cuba, 1 female from Florida, and 4 males from Florida. Right row from top: *Asio. f. flammeus*; 3 females from mainland southern Florida, 1 female from Grand Turk. Photograph by Reed Bowman.

tillean birds in wing length and back color and pattern, but had paler underparts and smaller bills. He did not assign them unequivocally to any named population.

Comparison of southern Florida specimens with Cuban specimens.—Five of the eight Florida owls not referable to *A. f. flammeus* were compared with the unsexed Cuban specimen (MNHN 1595), and all eight were compared to the second Cuban specimen (GEW 5925). The first four males from Florida had somewhat paler underparts than the first Cuban specimen (MNHN 1595), but the Florida female (GEW 5889) had slightly darker underparts. As is true for *A. f. flammeus* (Holt and Leasure 1993), females of the Antillean form may have darker underparts than males. The second Cuban specimen (GEW 5925) has some darker markings dorsally than most of the Florida specimens but otherwise appeared similar. The Florida specimens also agreed in detail with the Cuban specimens in the foot-feathering characteristics. We conclude that these eight specimens from southern Florida are vagrants from the Greater Antilles, and probably originate from Cuba. We suspect the slightly paler underparts and smaller bill size noted by Marshall are characteristics of age or sex.

Analysis of photographs.—The photographs of six owls from Florida agree in plumage with the eight specimens described above, so we consider them Antillean (Table 1). The first of these was discovered by Hoffman on Bush Key, Dry Tortugas, on 21 June 1978 and photographed in the hand by Barbara Kittleson (Hoffman et al. 1979). When the 1990 specimen was recognized as resembling Antillean representatives of the *Asio flammeus* species-group, we re-examined the photographs and found them to show the dark back and finely streaked buffy underparts of Antillean birds. The second owl was photographed by Howard P. Langridge in April 1985 (Kale 1985). It shows extensive black surrounding the eyes, and very fine streaking on the breast, indicating it is likely a juvenile and of Antillean origin. The third owl was photographed by Paul Cavanagh on Bottle Key, in northeast Florida Bay, on 24 August 1987. His photographs show the characteristic unstreaked back and lightly streaked belly of Antillean birds. The fourth owl, photographed by Hoffman at Ft. Zachary Taylor, Key West on 4 April 1994, also shows the unstreaked back, lightly streaked belly, and the sparsely feathered feet of Antillean birds, as well as the black feathering around the eyes seen on the five presumed juvenile male specimens. The fifth owl is the first of seeming Antillean origin found north of southernmost Florida. The bird was rescued from the surface of the Gulf of Mexico about 110 km west of Hernando Co (northwest of St. Petersburg) in early June 1994. It was photographed, rehabilitated, and eventually released by the Birds of Prey Center of the Florida Audubon Society. The sixth owl was photographed 29 April 1997 on Garden Key, Dry Tortugas, by Darlene Friedman and the photograph was forwarded to us by Paul Lehman; it also appears to be Antillean. We suspect that most of the other recent reports from the Florida Keys and Dry Tortugas also are of Antillean birds. Descriptions from the observers generally support this contention. Table 1 includes one *A. f. flammeus* specimen (collected 10 December 1992) and two sightings that may belong to this race (24 November 1979, winter 1983–84).

DISCUSSION

We document the occurrence in southern Florida of representatives of a population of the Short-eared Owl previously unrecorded from the North American continent. The documentation includes eight specimens and numerous photographs of several birds. The only taxon of this species previously known to occur on the continent is the Holarctic nominate race *Asio flammeus flammeus.*

Based on the characteristics of the specimens now available, we are confident that these owls are from the Greater Antilles. On geographical and historical grounds they most likely come from Cuba. Seven of our specimens, and perhaps most of the other southern Florida birds, appear to be juveniles and to have arrived during post-fledging dispersal. Breeding by Short-eared Owls is known to occur in Hispaniola and Cuba during northern hemisphere winter. Albert Schwartz collected nestlings in the Dominican Republic in November (LSUMZ 142354 and 142355), and Garrido (1984) reported a nest with eggs in Cuba on 8 December. Based on seasonality of reports, this pattern of dispersal to southern

Florida appears to be quite recent, beginning in the late 1970s.

Nomenclature of Antillean Short-eared Owls.—Assigning a scientific name to the owls invading southern Florida is a problem because the nomenclature of the Antillean Short-eared Owl is confused and poorly documented. Briefly the history is as follows. Muller (1776, reviewed in Wetmore 1928) described an owl from Hispaniola, based on Buffon (1770), as *Strix domingensis.* Subsequent authors ignored this taxon, or assumed it was based on the Burrowing Owl (*Athene cunicularia*) until Wetmore (1928) examined one short-eared owl each from the Dominican Republic and Haiti, and concluded these were examples of the subject of Buffon's illustration and account. However, prior to Wetmore's work, Ridgway (1882) described similar owls from Puerto Rico as *Asio portoricensis.* Wetmore (1928) compared his two specimens from Hispaniola to five from Puerto Rico, and concluded that those from Hispaniola were only subspecifically distinguishable from the Puerto Rican specimens. He used the names *Asio domingensis domingensis* and *A. d. portoricensis,* respectively. We find no publication that proposes and explains the merger of these taxa into *Asio flammeus.* Although Wetmore and Lincoln (1933) treated *domingensis* as a distinct species, only three years later Bond (1936), without explanation, listed these Antillean owls as subspecies of *A. flammeus.* This treatment seems to have been followed by most subsequent authors including Peters (1940). The situation is further confused because some recent authors have grouped the Hispaniolan (*domingensis*) and Puerto Rican (*portoricensis*) populations together, also without comment. Voous (1988) and Holt and Leasure (1993), for example, referred to all Antillean Short-eared Owls as the race *portoricensis* of *A. flammeus* despite the fact that the name *domingensis* seemingly has priority over *portoricensis* (Wetmore 1928). The existence of a Cuban breeding population has been recognized only since 1981, and no formal determinations of its taxonomic status have been published. Pending further study, we recommend using the single epithet *domingensis* for all the Antillean populations; Wetmore's (1928) justification for maintaining *portoricensis* separate from *domingensis* seems insufficient given his sample sizes.

We feel that the systematics and nomenclature of the Short-eared Owl are in need of revision. The validity of several races is inadequately established, in South America as well as in the West Indies. We also suspect that *Asio flammeus* may deserve splitting into two or more species. Ideally, such a revision would include detailed analyses of vocalizations, as well as studies of molecular genetic differences. The West Indian birds are among the most distinctive in plumage and structure, but the Galapagos race and the South American populations could plausibly deserve species status as well.

Biogeographic considerations.—The recent occurrence and increasing frequency of these owls in Florida raises the possibility of a new, northward colonization from the Antilles. Owls that reach mainland Florida may find habitat suitable for nesting. Nesting habitat in Cuba apparently includes pasturelands, rice fields (Garrido 1984), and sugar cane plantations (Garrido, pers. comm.). Habitats similar to all of these occur extensively in southern Florida.

If these Antillean owls colonize southern Florida, they will be part of an ongoing wave of colonizations from the West Indies. When Howell's *Florida Bird Life* was published (Howell 1932), the breeding landbird fauna of southern Florida contained only five species' populations clearly of West Indian origin: White-crowned Pigeon (*Columba leucocephala*), (Cuban) Mourning Dove (*Zenaida m. macroura*), Mangrove Cuckoo (*Coccyzus minor*), Gray Kingbird (*Tyrannus dominicensis*), and Black-whiskered Vireo (*Vireo altiloquus*). Robertson and Kushlan (1984), in their insightful analysis of the southern Florida avifauna, considered all these to be quite recent immigrants, in part because none showed geographic variation in Florida. A sixth and seventh species, Zenaida Dove (*Zenaida aurita*) and Key West Quail-Dove (*Geotrygon chrysia*), were reported breeding in the Florida Keys prior to 1850, but both now occur only as vagrants.

Since 1932 southern Florida has experienced an average of about one natural landbird invasion per decade from the West Indies. These recent immigrants are Smooth-billed

Ani (*Crotophaga ani;* Sprunt, A. Jr. 1939, 1954), Cuban Yellow Warbler (*Dendroica petechia gundlachi;* Greene 1942), Antillean Nighthawk (*Chordeiles gundlachii;* Greene 1943), Fulvous Whistling-Duck (*Dendrocygna bicolor;* reviewed by Palmer 1976, Turnbull et al. 1989), Cave Swallow [*Hirundo fulva cavicola* (= *H. f. fulva?*); Smith et al. 1988], and Shiny Cowbird (*Molothrus bonairiensis;* Smith and Sprunt 1987).

Most of these invading species had been known as vagrants to southern Florida for some time, and reports became increasingly frequent before breeding in Florida was documented. This fits a general, but often overlooked rule: range expansion tends to be driven by population dynamics (often population increases) in the source areas, rather than by habitat changes or initial reproductive success in the colonized areas.

Several West Indian birds, in addition to these owls, seem poised to invade Florida from the south or east (Bahamas). La Sagra's Flycatcher (*Myiarchus sagrae;* Smith and Evered 1992), Bahama Mockingbird (*Mimus gundlachii*), and Thick-billed Vireo (*Vireo crassirostris*; Smith et al. 1990) seem to be increasing in frequency as vagrants. Pearly-eyed Thrasher (*Margarops fuscatus*) has not been documented in North America as of this writing, but it has been extending its range northward in the Bahamas in recent years and could begin appearing in Florida in the near future. The Cuban subspecies of American Kestrel (*Falco sparverius sparveroides*) also has been expanding its range in the Bahamas, and recently was photographed by WH at Key West. Robertson and Kushlan (1984:226) speculated on potential immigrant West Indian species, naming "the Masked Duck, a hummingbird, Bahama [*Tachycineta cyaneoviridis*] and Cave swallows, Bananaquit [*Coereba flaveola*], Stripe-headed Tanager [*Spindalis zena*] and Black-faced Grassquit [*Tiaris bicolor*]" most likely. Of these, the Cave Swallow and possibly the Masked Duck (Bowman 1995) already have colonized.

The rate of immigration in recent decades, then, must be much higher than the overall post-Pleistocene rate, unless prehistoric extinction rates for immigrant populations were extremely high. The Zenaida Dove and Key West Quail Dove, once reported to breed in the Florida Keys, no longer do so. These possible extirpations of breeding populations most likely resulted from hunting and habitat destruction (Robertson 1978a, 1978b; Robertson and Woolfenden 1992).

The apparent increase in immigration rates from the West Indies to Florida may have resulted from anthropogenic changes in the environment, both in the West Indies and in Florida. Habitat changes, associated with forest clearing for grazing, cultivation, and urban development, and global climate changes are two nonexclusive anthropogenic changes to the regional environments that could drive these colonizations. All the known Cave Swallow colonies in Florida, for example, are located on concrete bridges and overpasses along highways (Smith et al. 1988), so the increase in numbers of vagrants prior to colony establishment (Robertson and Woolfenden 1992) must have reflected population or habitat changes in Cuba.

Explanations for northward colonization involving global climate change potentially can explain both the recent wave of colonizations and the dearth of West Indian birds in the southern Florida avifauna prior to this century. A global warming trend has been underway since the end of the "Little Ice Age" in about 1870 (Pielou 1991), a trend that has accelerated because of increases in atmospheric carbon dioxide, methane, and other greenhouse gasses (Maul 1989). Some West Indian birds may have colonized the Florida peninsula previously during the Holocene, but stopped during the "Little Ice Age". Although records are inadequate or nonexistent, the lower average temperatures of the "Little Ice Age" likely were manifested in southern Florida by more frequent and more severe episodes of cold winter weather rather than by cooler summer weather. These hypothetical cold episodes could have been particularly damaging to West Indian bird populations attempting to persist in southern Florida. The current warming trend also may be fueling population increases in the West Indies for the species that have recently colonized, or are appearing more frequently as vagrants. This warming trend also may be making southern Florida habitats subtly more suitable for these birds (Robertson and Kushlan 1984).

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